

ECHINODERM CALCITE: A MECHANICAL ANALYSIS FROM LARVAL SPICULES

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ABSTRACT

The flexural stiffness (EI) was measured for simple and fenestrated spicules in echinoid larvae. A Young's modulus (E) of 36.3×10^9 N/m² was estimated for these calcitic spicules by EI/I where I was calculated independently from measurements made by SEM. The flexural stiffness of fenestrated spicules is approximately three times greater than that of simple spicules. This increased flexural stiffness is due to structural and not material differences between the spicules. At the material level, this calcitic tissue behaves like a composite which will reduce stiffness but increase strength compared to inorganic calcite. At the structural level its porous nature increases its stiffness and buckling strength over that of a solid structure of similar weight. These characteristics should also increase the tensile strength of this skeletal component and increase its usefulness as a strong, stiff element in most echinoderm skeletons.

INTRODUCTION

This paper discusses the mechanical properties of echinoderm calcitic tissue (hereafter echinoderm calcite) at the material, structural, and skeletal levels. I present results of bending studies on simple and fenestrated spicules of echinoid larvae. These spicules have the same composition and manner of formation as adult calcitic structures (e.g., Okazaki and Inoué, 1976; Loeper and Pearse, 1981). The simple shape of larval spicules facilitates the measurement of the mechanical properties of echinoderm calcite. The results provide evidence that echinoderm calcite is a composite material and exemplify the consequences of arranging this material into porous structures. In the discussion I generalize the findings of this study to adult structures and propose new ideas which may help explain the unusual structure of echinoderm calcite. This treatment expands the known mechanical role of echinoderm calcite beyond withstanding compressive loads.

MATERIALS AND METHODS

Echinoplutei with simple and fenestrated skeletons were reared in culture or obtained from the plankton near Friday Harbor, Washington. Culture methods are adapted from Hinegardner (1967) and Strathmann (1971). Spicules from larvae of *Strongylocentrotus droebachiensis* O. F. Muller, *Strongylocentrotus franciscanus* A. Agassiz, and *Dendraster excentricus* Eschscholtz were isolated with 5% sodium hypochlorite (Chlorox Bleach) and washed three times with distilled water. Adult calcitic structures from the holothurian, *Psolus chitonoides* H. L. Clark were isolated by a similar method.

Definitions of mechanical terms are as follows:

- σ : Stress—force/cross-sectional area, where the force acts over that area. Units: N/m^2 .
- ϵ : Strain—change in length/original length, where change in length is produced by a stress. Units: dimensionless or m/m .
- E : Young's modulus—the stiffness of a material, σ/ϵ . The stress in a material is divided by the strain produced under stress. Units: N/m^2 .
- I : Second moment of area of a cross-section is a description of the geometric distribution of material around a neutral axis of bending. $I = \int y^2 dA$ where dA is area of material at distance y from the neutral axis (see Wainwright *et al.*, 1976). For a circular cross-section $I = 1/4 \pi r^4$ where r = radius. Units: m^4 .
- EI : Flexural stiffness of a structure—the product of Young's modulus and the second moment of area which describes the ability of a structure to resist bending. Units: Nm^2 .

EI may be used to compare structures which vary in material or shape, and is especially useful when shapes are complex. If either E or I and flexural stiffness are known, then the other variable may be determined. In this study EI is determined for spicules from small scale deflections of two cantilevers: a glass microneedle whose flexural stiffness was determined separately and an experimental spicule. Made from a fiber of fiberglass, the microneedle was $10 \mu\text{m}$ in diameter and 1 mm long and was fixed to the end of a 3 mm diameter glass rod. The flexural stiffness of the needle was determined by calculating I from dimensions and E from equations of bending for a simply supported beam (Gordon, 1978). Known weights (0.2 and 0.5 mg) were hung on the needle and vertical deflection, measured in μm , was photographed with a horizontally oriented photomicroscope. E for the needle is 60 GN/m^2 .

For measurement of spicule stiffness, a cantilevered spicule was fixed over the edge of a microscope slide with Eastman 910 cement. The needle and spicule were aligned horizontally in the focal plane under a photomicroscope, and the stage was moved so that the needle bent the spicule. Multiple exposure photos were taken because they increase the accuracy in measuring deflection of the needle (Fig. 1). The photographs were analyzed by superimposing the undeflected spicule over the deflected spicule, and then measuring the length of both cantilevers to point of contact and the distance from this point to the identical point on each undeflected cantilever (see Fig. 1). The force exerted on the deflected spicule is equal to that exerted on the deflected needle, so flexural stiffness was determined by solving cantilever bending equations (Gordon, 1978) as follows.

$$F_n = 3(E_n I_n Y_{n\text{max}})/L_n^3 = F_s = 3(E_s I_s Y_{s\text{max}})/L_s^3$$

where

- F_n = force exerted by the needle of the spicule (Units: N)
 F_s = force exerted by the spicule on the needle (N)
 E_n = modulus of the glass (N/m^2)
 E_s = modulus of the spicule (N/m^2)
 I_n = second moment of area of the needle (m^4)
 I_s = second moment of area of the spicule (m^4)
 $Y_{n\text{max}}$ = deflection of the needle where it contacts the spicule (m)
 $Y_{s\text{max}}$ = deflection of the spicule where it contacts the needle (m)
 L_n = length of the needle to point of contact with spicule (m)
 L_s = length of the spicule to point of contact with needle (m)

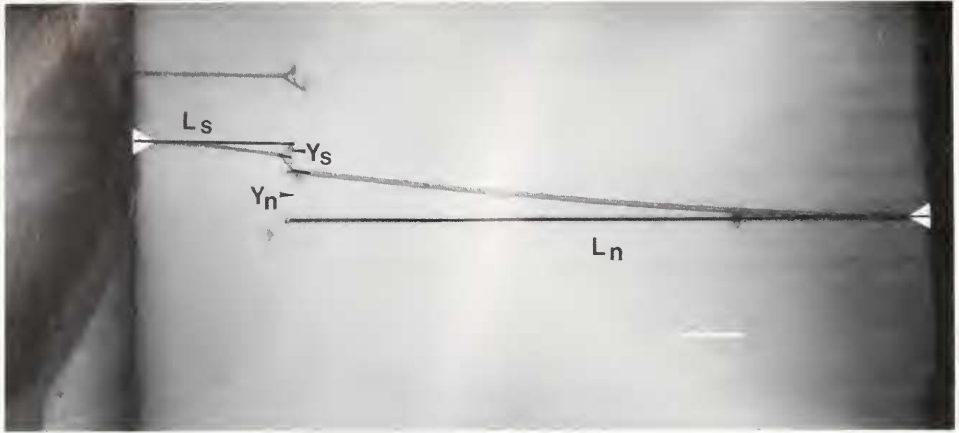


FIGURE 1. Stiffness measuring technique, a double exposure. The spicule was moved to contact and bend the stationary needle, and the first exposure was taken. Then the spicule was moved free of the needle, and a second exposure was taken. The image of the undeflected spicule was then drawn onto the photo. Dimensions were taken from the photographs. Black lines show the length of the cantilever needle, L_n , and spicule, L_s . Y_n and Y_s are the distances of deflection of the needle and spicule respectively. See text for further explanation. Scale (white line): 0.1 mm.

This equation can be rewritten in the following way:

$$E_s I_s = (Y_n/Y_s) \cdot (L_s/L_n)^3 \cdot (E_n I_n)$$

Only bends where Y_n/L_n and $Y_s/L_s \lesssim 10\%$ were used because this equation is not accurate for larger deflections where shear in the material becomes increasingly important (FaupeL, 1964). No attempt was made to measure breaking strength.

For simple spicules which are circular in cross-section, $I = 1/4 \pi r^4$ with r = radius of the spicule. For the fenestrated spicules, $I = 3/4 \pi r^4 + 3/2 \pi r^2 d^2$, with r = radius of the element rods and d = radius of the spicule. The amount (volume) of skeletal material in larval spicules was also estimated with dimensions taken from SEM photos. I treat the fenestrated spicules as three parallel circular cylinders joined by cross-ties.

Other mechanical calculations will be introduced as needed in the discussion. They are taken from Wainwright *et al.* (1976) and FaupeL (1964), and may be found in most general mechanical engineering texts.

RESULTS

The spicules of echinoplutei reared during this study are 500 to 800 μm long. Simple spicules range in diameter from 2 to 4 μm . Each of the three elements of fenestrated spicules are 1.5 to 2.5 μm in diameter and the whole spicule is 5 to 10 μm in diameter (Fig. 2). Fenestrated spicules contain about twice as much material as simple ones of similar length. In a fenestrated spicule the material is located farther from the bending axis, so these spicules should be stiffer than simple spicules. An empirical measure of stiffness rather than calculation of I is used for three reasons. For fenestrated spicules the tapering width and irregular spacing of cross-ties make accurate calculation of I difficult. These spicules are stiffest at the base where the spicule enters the body region of the larva. There is also a slight twist in the member elements of the fenestrated spicule of *Dendraster* (Fig. 2f, g). This 60° rotation is in the same direction for all four of the fenestrated spicules in a larva.

Fenestrated spicules are about three times stiffer than simple spicules (Fig. 3; Mann-Whitney U test, $P < 0.001$). The mean stiffness measured for fenestrated is $14.1 \times 10^{-13} \pm 2.2 \times 10^{-13}$ s.e. and mean stiffness for simple spicules is $3.8 \times 10^{-13} \pm 0.6 \times 10^{-13}$ s.e. Nm^2 . I report only two data points for the simple spicules of *Dendraster*, but these fall in the same range for simple spicules of *S. franciscanus*. The large variation in EI of the fenestrated spicules (Fig. 3) is probably due to a large variation of I .

The calculated Young's modulus of calcite is $36.3 \text{ GN/m}^2 \pm 2.9 \text{ GN/m}^2$ s.e. ($n = 4$) in the simple spicules which were straight and had a constant diameter. The E calculated for one fenestrated spicule is 48.9 GN/m^2 . No other values of E for fenestrated spicules were determined because of the difficulty of accurately calculating I .

Figure 4 shows some of the calcitic structures found in *Psolus chitonoides*. These structures are typical of those found throughout adult echinoderms.

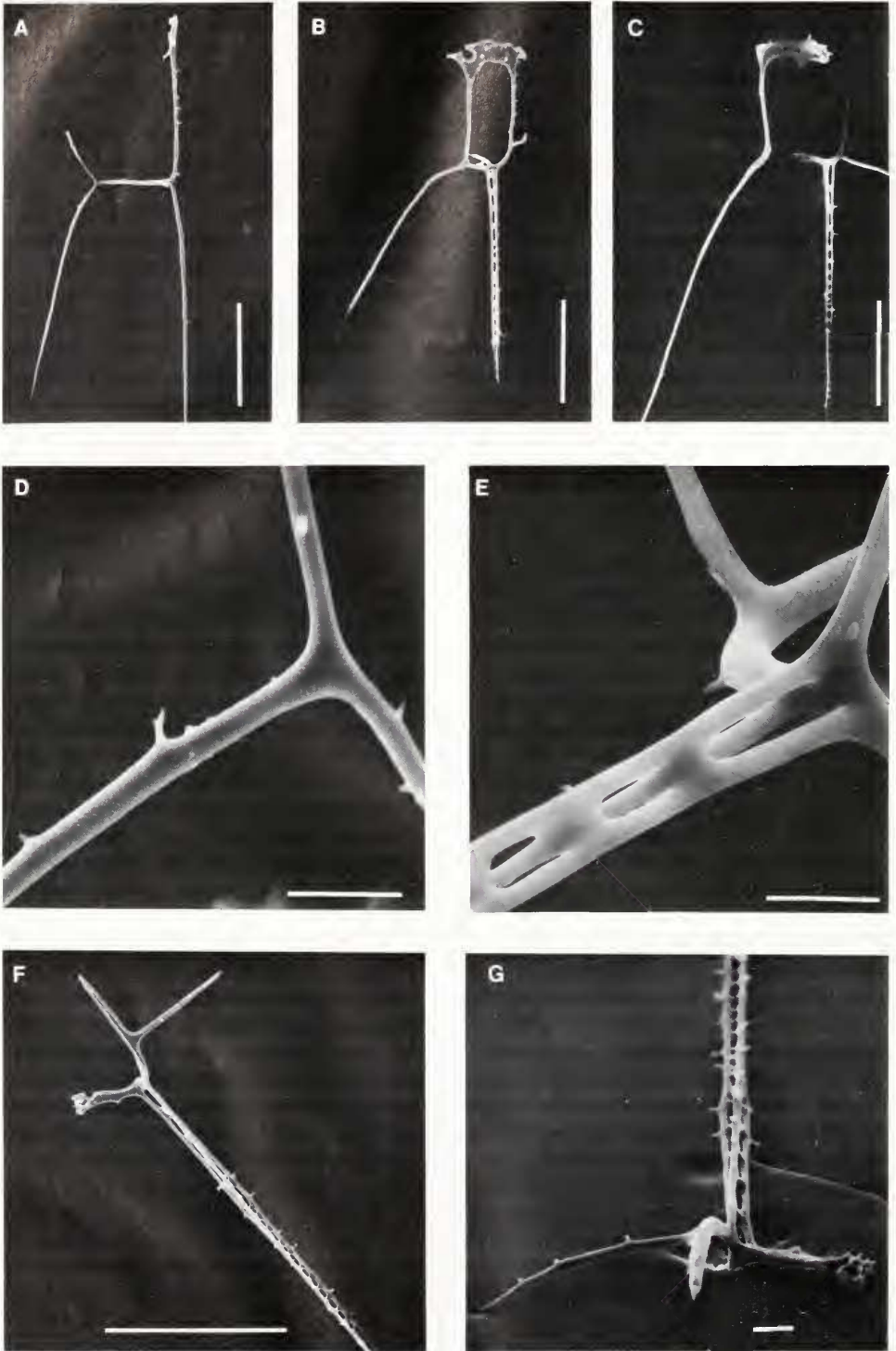
DISCUSSION

The material

In this study Young's modulus (E) of echinoderm calcite is determined to be 36.6 GN/m^2 (s.e. = 2.9, $n = 4$). This value is lower than all previous reports except one. Burkhardt and Märkel (1980) give values for E in diademid spines as 69.4 and 52.1 GN/m^2 for dry and wet spines, respectively. Currey (pg. 167 in Wainwright *et al.*, 1967) gives values of 74 and 9.7 GN/m^2 in spines and plates of echinoids, respectively. Differences may be due to methodological difficulties of measuring E and I in previous studies. All of these studies including the present one calculate E from EI/I where I is estimated from cross-sections through the structure and is exclusive of voids in the material. Determination of I can be difficult especially for structures which have a complex distribution of material around a bending axis as in echinoderm stereom, the adult skeletal plate structure. It is possible that E values previously reported differ from what is found here because the I was inaccurately calculated. When I is calculated from dimensions on a photograph, the E is greater for a fenestrated spicule than that for a simple spicule. This is due to an underestimate of I , probably due to difficulties of evaluating I at cross-ties. It is not likely that fenestrated spicules are made from a different calcitic material. The simple and fenestrated spicules in *Dendraster* grow out of the same triradiate spicule, and simple spicules have approximately the same E and I as simple spicules from *S. franciscanus*.

As a material, echinoderm calcite should no longer be considered similar to inorganic calcite. The single crystal construction suggested by optical behavior (*e.g.*, Donnay and Pawson, 1969) is more apparent than real. Several authors (Travis, 1970; Pearse and Pearse, 1975; Okazaki and Inoué, 1976; Urakami *et al.*, 1980; O'Neill, 1981) provide evidence for an oriented microcrystalline construction. In addition, all of the reported values for Young's modulus are two to four times lower than that expected for inorganic calcite (137 GN/m^2 , Bhimasenachar, 1945). These two differences suggest that there is an organic matrix in echinoderm calcite.

The mechanical properties of a crystalline material may vary with the orientation of the crystal. The modulus of inorganic calcite is 137 GN/m^2 in the direction of the C-axis but is as low as 34.2 GN/m^2 in the other directions (Bhimasenachar, 1945). Okazaki and Inoué (1976) confirmed that the C-axis in most larval spicules is in the long axis of the spicule. Raup (1966) reports the same for the orientation in spines, but reports that the C-axis may be perpendicular or tangential in echinoid



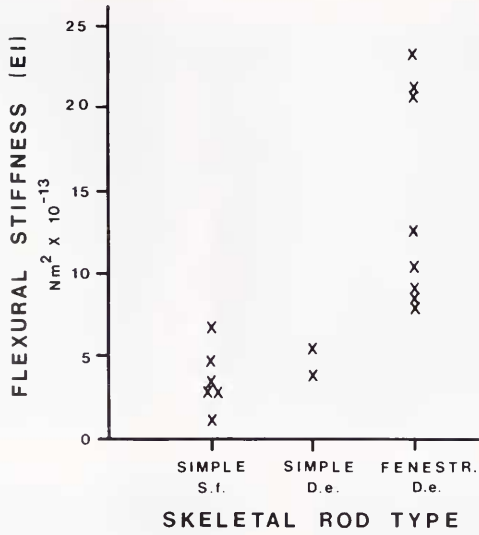


FIGURE 3. Flexural stiffness (Newtons \times meter² $\times 10^{-13}$) of simple and fenestrated spicules. Mean EI of simple spicules: 3.8×10^{-13} N/m², s.e. 0.6. Mean EI of fenestrated spicules: 14.1×10^{-13} , s.e. 2.2. The stiffnesses of the two spicule types are significantly different, Mann-Whitney U test, $P < 0.001$. S.f., *Stronglyocentrotus franciscanus*; D.e., *Dendraster excentricus*.

plates. The orientation of the C-axis along the long axis of these structures means that they are stiffer than they would be if the C-axis were in any other orientation. With the possible exception of the value for the plate, the lower stiffness of echinoderm calcite cannot be attributed to varying C-axis orientation.

Magnesium replaces up to 16% of the calcium in echinoderm calcite, but the reasons for the variation in magnesium content remain obscure (Chave, 1954; Weber, 1969). It is not clear how magnesium content will affect the modulus. Increasing magnesium content increases the hardness of calcite (Wainwright *et al.*, 1976) and therefore will probably increase stiffness.

A porous microstructure would explain the reduced stiffness. Okazaki and Inoué (1976) showed a high magnification SEM photo suggesting a porous surface on carefully isolated spicules. Observation under high magnification of the spicules isolated by my own techniques never revealed that apparent texture. An empirical formula (by Mackenzie, pg. 157 in Wainwright *et al.*, 1976) for change in modulus in a porous ceramic predicts that a 50% volume of pores is necessary to give a 75% reduction in modulus, equivalent to the E reported here. Therefore, a porous microstructure probably cannot account for the reduced stiffness of echinoderm calcite.

An organic matrix and composite construction would also reduce the stiffness of the calcitic tissue. Though the collagen connecting the calcitic plates may contaminate some samples (Klein and Currey, 1970; Travis, 1970), there is growing evidence for an organic matrix in echinoderm calcite (Klein and Currey, 1970;

FIGURE 2. Simple and fenestrated calcareous spicules isolated from echinoplutei. (A) Simple "half skeleton" of two week old *S. franciscanus*. (B, C) Early and later stages of the fenestrated "half skeleton" of *D. excentricus*. In (C) the skeleton is modified and allows articulation of the fenestrated post-oral rod. A, B, C, scale 100 μm . (D, E) Higher magnification of the simple and fenestrated spicules. Note the smooth surface of the calcite. D, E scale: 10 μm . (F, G) Fenestrated spicules of *D. excentricus*. (F) Note the taper and irregular spacing of cross-ties in fenestration. Scale: 100 μm . (G) Same spicule as (F), note the twist in the parallel elements of the fenestrated part. Scale: 10 μm .

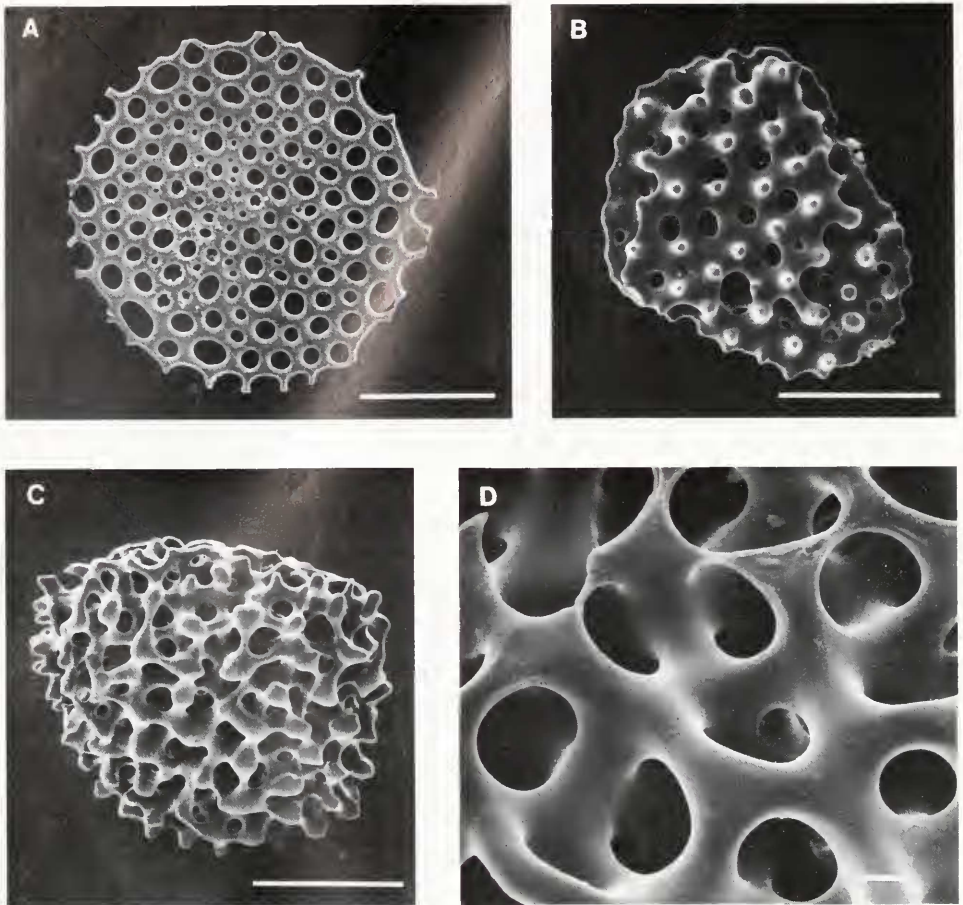


FIGURE 4. Plates and stereom of the holothurian *Psolus chitonoides*. (A) Flat plate. Scale: 100 μm . (B) A plate that is becoming a laminated structure with the addition of a new layer. Scale: 100 μm . (C) Labyrinthic stereom structure in the form of a block. Scale: 100 μm . (D) Higher magnification of a stereom surface. Scale: 10 μm .

Travis, 1970; Pucci-Minafra *et al.*, 1972; Pearse and Pearse, 1975; Okazaki and Inoué, 1976). Okazaki and Inoué (1976) give an organic content for the larval spicules of about 1% by weight. Klein and Currey (1970) give a value of 0.3% protein by weight (about 1% by volume) which is close to the 0.36% for protein in larval spicules given by Okazaki and Inoué (1976).

Evidence for a highly oriented microcrystalline structure in echinoderm calcite is also increasing. Polarized light and X-ray diffraction studies (Raup, 1966; Donnay and Pawson, 1969; Nissen, 1969) suggest that echinoderm calcite is a single crystal, but these studies cannot distinguish between a single crystal and a highly ordered microcrystalline construction where all the microcrystals have the same C-axis orientation. Fracture studies do not show cleavage planes expected of inorganic crystalline calcite (Raup, 1966; Nichols and Currey, 1968; Nissen, 1969; Okazaki and Inoué, 1976), and several authors show fractures (Pearse and Pearse, 1975; O'Neill, 1981) or etching (Okazaki and Inoué, 1976) which suggest concentric laminated ordering of microcrystals. Recent studies by O'Neill suggest that when echinoderm

calcite is stressed in tension the microcrystals creep, or move with respect to one another. Currey (1965) loaded echinoid spines in bending and found no creep after 26 h. But, as he states, the spines were from dried specimens, which may have prevented creep from occurring.

If, in fact, this calcite tissue is a highly ordered "inorganic polycrystalline aggregate" (Travis, 1970) bound in a very small amount of organic matrix (1 to 2% by volume), then mechanically its behavior can be treated as a composite material. In this treatment the microcrystals are analogous to short fibers and the organic material is the matrix which binds them. The modulus, E_c , of the composite, modeled as a series of layers of fibers and matrix can be predicted as follows:

$$1/E_c = V_f/E_f + V_m/E_m$$

where

V_f = volume fraction of fibers = 99%

E_f = modulus of fibers = 137 GN/m²

V_m = volume fraction of matrix = 1%

E_m = modulus of matrix = 0.6 GN/m²

and $V_f + V_m = 1$

(Currey, pg. 145 in Wainwright *et al.*, 1976. The value of the modulus for the matrix is that of human tendon and is meant to be an approximation to the collagen-like component of matrix.)

By this formula E_c is evaluated to be 41.9 GN/m² which is one standard deviation higher than the value of 36.3 GN/m² determined in this study. Therefore, it may be reasonable to treat the material, echinoderm calcite, as a special kind of composite with a high fiber content. Although this formula is used to model composites whose components are arranged in series (Reuss model), there is no evidence that components in echinoderm calcite are physically arranged in this way. The formula merely predicts this composite's behavior. Echinoderm calcite has been called a composite by Weber *et al.* (1969), but the present work is the first to describe its mechanical behavior as a composite material.

Biological implications

Comparison of the mechanical properties of echinoderm calcite with that of inorganic calcite reveals the biological advantages in composite construction. A spicule of composite construction should be effectively stronger than one constructed from a single inorganic crystal. In theory the inorganic calcite should have a higher fracture stress (greater force per unit area at failure), but in practice tiny cracks and surface flaws set the upper limit to fracture stress (Wainwright *et al.*, 1976). A composite construction of many tiny crystallite 'fibers' may reduce the possibility of this common cause of failure in brittle materials if cracks are not propagated through the material when a single or a few fibers break (Wainwright *et al.*, 1976; Gordon, 1978).

Brittle materials are usually weaker in tension than compression. This restricts the usefulness of such a material to sustaining compressive loads. The composite construction should increase the tensile strength over that of inorganic calcite. Fractures caused by rapid loading usually do not show inorganic fracture planes, which would require the lowest work of fracture. In a composite material, in which the modulus of the fibers and the viscosity of the matrix are high, rapid loading should crack through matrix and fiber, but under low and even stress, the matrix would

be expected to shear. O'Neill's (1981) pictures of microcrystals in prestressed fracture support this prediction of material behavior.

The larval spicules

Arm rods of echinoderm larvae are the simplest echinoderm skeletons and, therefore, are a good starting place for the analysis of mechanical properties at the structural level. If E is the same for all echinoderm calcite, then comparison of stiffness for different structures can be made through their I values. (Compare $I = 3.9 \times 10^{-23} \text{ m}^4$ for fenestrated spicules with $I = 1.2 \times 10^{-23} \text{ m}^4$ for simple spicules.) While the I of fenestrated spicules is approximately three times as much, they contain only twice as much calcite as simple spicules. If the same volume of material that is in a fenestrated spicule were arranged in a simple structure around the bending axis, its I value would be about twice that of the simple spicule. Fenestration gives the spicule an increased stiffness per amount of material. Further, a solid spicule constructed with the same dimensions as a fenestrated spicule would increase the stiffness by an order of magnitude over the simple spicule but would also require about six times the amount of material. The use of less material must be important in a planktonic larva which has to overcome gravity to stay afloat.

Other benefits of fenestration can be appreciated by looking again at the structure (Fig. 2e, f, g). Three parallel rods are the minimum above one which give almost even stiffness around a central bending axis. Two parallel rods will not provide an even distribution of I . The left-handed twist of about 60° in the parallel elements reduces stress along any rod when the spicule is bent in a certain direction. This slight twist, in the same direction for all fenestrated spicules in *Dendraster* larvae, probably reflects the construction pattern or orientation of the organic matrix. This pattern cannot be the result of net torque on the arm due to swimming currents, because the mirror image pairs would have opposite coiling twists since the currents are subject to bilateral symmetry.

Fenestration increases stiffness in torsion about a central axis. Here cross-ties increase the J value (second polar moment of area), which is a measure of the geometric distribution of material around a twisting axis and is analogous to the I value. Fenestration also increases the resistance to buckling since it is proportional to flexural stiffness. Functions of the larval skeleton will be discussed in more detail in a later paper.

The adult skeleton: porous plates and stereom

The mechanics of the unusual structure of the adult skeletal plates, called stereom (Fig. 4c,d), have been largely uninvestigated. Nichols and Currey (1968) suggest that the porous structure may strengthen echinoderm calcite since small cracks stop when they run into a hole and also point out that this construction allows access to surfaces for repair. As in the composite construction, the porous structure should reduce the difference between strength in tension and strength in compression. Currey (1975) compared the crushing strength of echinoderm stereom with that of mollusc shell and found it comparable to moderately strong mollusc shell on a unit weight basis. The crushing strength for echinoderm stereom is 50–100 MN/m² (Wainwright *et al.*, 1976). However, I calculated a stress of 120 MN/m² at 14% tip deflection in an unbroken spicule during a bending trial (see Wainwright *et al.*, 1976, pg. 248, for formula of tensile stress in bending).

Like fenestrated spicules, the porous calcite structures of adults have the benefits of increased bending and torsional stiffness and buckling strength, when compared

on a unit weight basis with solid structures. For structures with the same general shape and composed of the same weight of material, stiffness will increase faster than strength with increasing porosity. This is because stiffness is proportional to I which is proportional to r^4 and strength is proportional to I/r or r^3 . I will be greater for complex stereom than for solid structures because material is separated in space around the bending axis (larger r). The largest I occurs if the material is distributed in an annulus about the central axis. This means that while there are no great differences in the strength to weight ratios of echinoderm stereom and mollusc shell, there are differences in the stiffness or buckling strength to weight ratios, with echinoderm skeleton being greater in both.

Mechanical properties may vary within and between skeletal blocks because of different stereom structure. Smith (1980) demonstrated a range of variation in pore density and pattern in the stereom structure of echinoids and described ten distinct stereom types. Macurda *et al.* (1978) described four of these types for recent crinoids. Figure 4 shows three of these types also found in the holothurian, *Psolus chitonoides*. Reoccurring stereom fabrics suggest the possibility of mechanical differences, but no work has demonstrated this. A more quantitative analysis is needed that will demonstrate how, for a given amount of material, stiffness and strength are influenced by porosity. This analysis may be done by comparing the different stereom structures by calculating I 's and cross-sectional areas of material in structures with the different stereom types. Carter and Hayes (1976) showed that different types of bone tissue can be treated similarly in mechanical testing, and that variation in compressive strength in bone of different tissue morphology can be described as a function of its relative density and the compressive strength of compact bone. Similar studies on echinoderm stereom should lead to development of formulae which describe strength or stiffness as a function of density and stereom type.

The skeletal system

The organization of these plates into functional skeletons for organs and organisms is highly varied. Skeletal blocks with different mechanical properties are arranged and interconnected more or less tightly with collagen fibers (Hyman, 1955) and often articulated with muscle. The nature of formation of these optical crystalline blocks inside a syncytium (Okazaki and Inoué, 1976; Loeper and Pearse, 1981) may account for the small degree of variation (mineral content) in the composite material echinoderm calcite. Structural differences may be viewed as the method of varying mechanical properties of calcite materials. Smith (1980) reported that galleried stereom is always associated with long bundles of collagen fibers. Macurda *et al.* (1978) found characteristic spines on the labyrinthic stereom where muscles attach. One of the intentions of Smith's (1980) study was to correlate stereom type with soft tissue type, but perhaps it may be more appropriate to correlate stereom type with mechanical operation.

The porous structure of echinoderm calcite increases its flexural and torsional stiffness, buckling strength, and possibly its tensile strength on a unit weight basis over that of a solid construction. A composite and porous construction may allow wider application of this element in skeletons than just carrying compressive loads. Eylers (1976) describes the distribution of forces in the skeleton of an asteroid during the opening of bivalve prey. The ossicles joined along the aboral surface by collagen and muscle are in tension, and ambulacral ossicles experience bending, torsion, and compression. Tensile forces also occur in the arms of suspension feeding crinoids and ophiuroids, spines of echinoids, imbricate plate systems, and most other ex-

amples of echinoderm skeleton. The mechanical behavior of an intact adult skeleton should then be analyzed as an interaction between composite blocks, collagen connective tissues, and muscle. The mechanical diversity of echinoderm skeletal organization may also be attributed to material and structural properties of echinoderm calcite.

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